

ROUTES AND TIMING OF MIGRATION OF FALCONS BANDED IN CANADA

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ABSTRACT.—We banded 6494 falcons, primarily (85%) in western Canada. Recovered falcons (235, 3.6%) included six Gyrfalcons (*Falco rusticolus*), 96 Prairie Falcons (*F. mexicanus*), 86 Peregrine Falcons (*F. peregrinus*), 44 Merlins (*F. columbarius*) and three American Kestrels (*F. sparverius*). Some Gyrfalcons, Prairie Falcons, and Merlins were recovered in Canada in winter. The migrating falcons generally moved through the North American interior. Prairie Falcons used two separate migration routes, one west of the Rocky Mountains and one east within grassland habitat. Recoveries suggest that Prairie Falcons did not fly the shortest distance to their wintering grounds. “Canadian” Prairie Falcons overlapped in their winter distribution with falcons banded at least 650 km south in Wyoming. Although widely dispersed outside of the breeding season, Prairie Falcons inhabited grasslands during migration and winter. Peregrine Falcons moved long distances, passing rapidly through Canada and the United States, and spent approximately seven months of the year outside of Canada along the Central American coasts and in South America. Some Merlins did not migrate. Sexual differences in the recoveries of Prairie Falcons could be attributed to differential mortality and not necessarily differences in migration. *F. p. tundrius* flew farther south than *F. p. anatum*, an example of “leap-frog” migration. Leap-frog migration was also suggested by one Merlin banded in the Yukon and recovered in Costa Rica. Received 2 Jan. 1990, accepted 25 May 1990.

We report here the banding and recovery locations of five species of falcons. Gyrfalcon (*Falco rusticolus*), Prairie Falcon (*F. mexicanus*), Peregrine Falcon (*F. peregrinus*), Merlin (*F. columbarius*), and American Kestrel (*F. sparverius*) were banded as part of toxicological studies and endangered species management (Fyfe 1976, Fyfe et al. 1976). In identifying the seasonal timing of movement, migration routes, and age and sex differences, we make a number of assumptions. First, we deduce the patterns of migration from banded falcons that were reported dead or captured alive. We assume that those falcons not encountered behaved similarly. Second, we assume that migratory behavior in these falcons is a heritable trait under the influence of natural selection, as it is in some other birds (e.g., Harris 1970, Berthold and Querner 1981). Third, we assume that the chance that a dead falcon was found did not vary throughout the year nor within an ecogeographic region (e.g., the North American Great Plains). However, differences may exist in the reporting rate of

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banded falcons between regions in North, Central, and South America based on human population density, nationality and habitat characteristics.

STUDY AREA AND METHODS

From 1967 to 1980, 6494 falcons of five species were banded in Canada under a master banding permit held by R. W. Fyfe. One recovered Gyrfalcon and 33 (38%) recovered Peregrine Falcons had been banded or released in central or eastern Canada (east of 90° longitude), but most Gyrfalcons and Peregrine Falcons were banded in the western Canadian Arctic and Subarctic. Eighty-nine (93%) Prairie Falcons, 29 (66%) Merlins and all three American Kestrels were banded in southern Alberta, the remainder in Saskatchewan. We categorized peregrines from north of the tree line in Canada as *F. p. tundrius*, those to the south as *F. p. anatum* (White 1968), and those on the Queen Charlotte Islands, British Columbia as *F. p. pealei*.

Most falcons (89–95%) were banded as nestlings, but some adults also were captured. Starting in 1974, Peregrine Falcons were equipped with color bands in addition to the standard metal leg bands. When a report of a banded falcon was received from the banding office, a questionnaire was mailed to the finder, requesting additional information on the condition of the falcon when found (freshly killed, partly decayed, fully decayed), the precise location, type of habitat and cause of mortality if known. For an analysis of timing of migration, we excluded recoveries of fully decayed falcons. In the case of 6 falcons which were reported partially decayed, we subtracted 30 days from a recovery date and proportionately less according to recovery latitude and season. Thirty-three Peregrine Falcons (38%) were raised in captivity and released into the wild. These were of *F. p. anatum* stock and were released in the boreal forest, parkland or eastern forest regions of Canada. For nestlings banded in the final third of the nestling period (approximately 80% of all nestlings), we assigned sex based on their size relative to nest mates and their age.

RESULTS AND DISCUSSION

Recovery rates.—A total of 235 of the 6494 banded falcons (3.6%) were recovered (Table 1). Many recoveries were near the banding site and provided little information about migration. Recovery rate varied among

TABLE 1

NUMBER OF FALCONS BANDED IN CANADA AND RECOVERED IN NORTH OR SOUTH AMERICA

	Gyrfalcon	Prairie Falcon	Peregrine Falcon	Merlin	American Kestrel	Total
Banded	301	3447	870	1419	457	6494
Recovered	6	96	86	44	3	235
(%)	(2.0)	(2.8)	(9.9)	(3.1)	(0.7)	(3.6)
Dead/injured	5	86	36	30	2	159
(%)	(1.7)	(2.5)	(4.1)	(2.1)	(0.4)	(2.5)
Live captured	1	9	36	14	1	61
Circumstances unknown	—	1	14	—	—	15

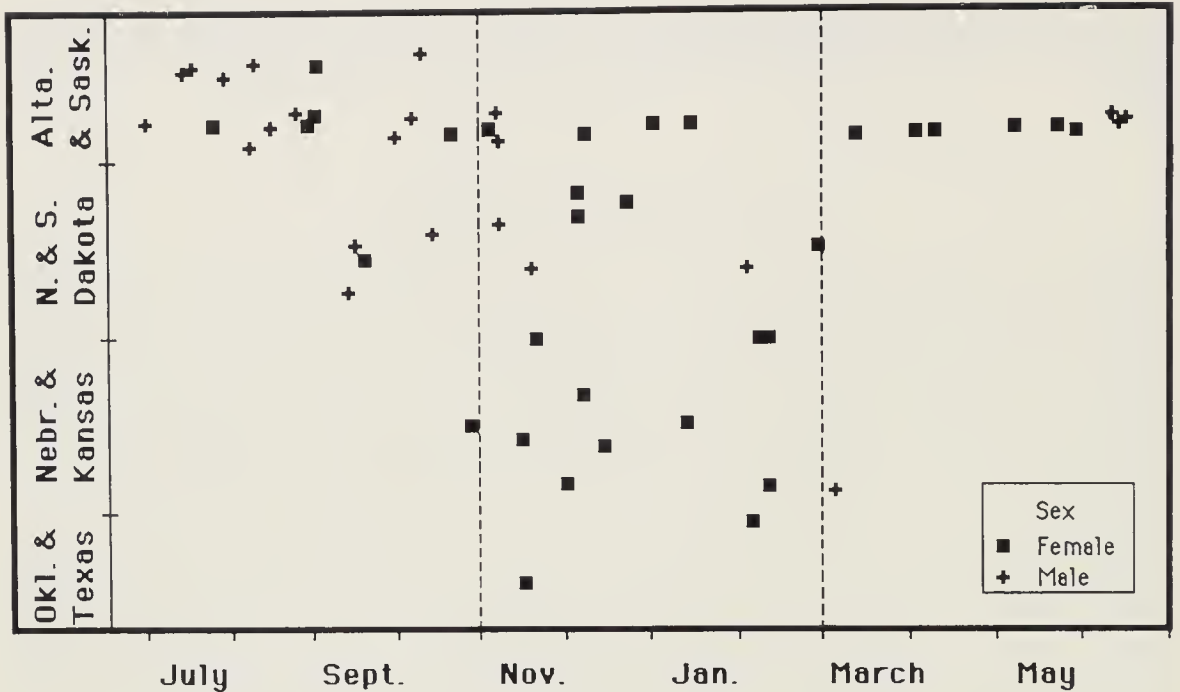


FIG. 1. Recoveries of male and female Prairie Falcons according to date and latitude. Broken, vertical lines delimit winter months (see text).

species from 0.7 to 9.9%. Thirty-six of the Peregrine Falcon recoveries were live captures, a result of the considerable trapping effort devoted to Peregrine Falcons (e.g., Ward and Berry 1972). When recaptured individuals were excluded the range of recovery rates narrowed to 0.4 to 4.1%. Even these recovery rates for dead falcons differed significantly between species ($\chi^2 = 19.61$, $P < 0.001$). Peregrine Falcons were most frequently recovered, possibly because they wore color bands. Kestrels were least frequently recovered presumably because their small bodies remained undetected more often than large falcons. Gyrfalcons had the second lowest rate, possibly because they frequented sparsely populated northern regions of Canada for most of the year. The observed rates of recovery were lower than those for raptors including owls banded in the United Kingdom, which ranged from 7–17% (Newton 1979:372). These differences probably reflect differences in encounter rates arising from differences in human population densities between Europe and the Americas, and only secondarily from differences in mortality rates.

Timing of migration.—Of six nestling Gyrfalcons, four were recovered between September and January, between 900 to 2400 km south or west of their nesting area. Two falcons were recovered near their nests. A sufficient number of Prairie Falcons, Peregrine Falcons, and Merlins had been reported as freshly killed, partly decayed or captured alive to permit an examination of the timing of migration. We defined the winter period for a species so that it encompassed those months in which at least 85%

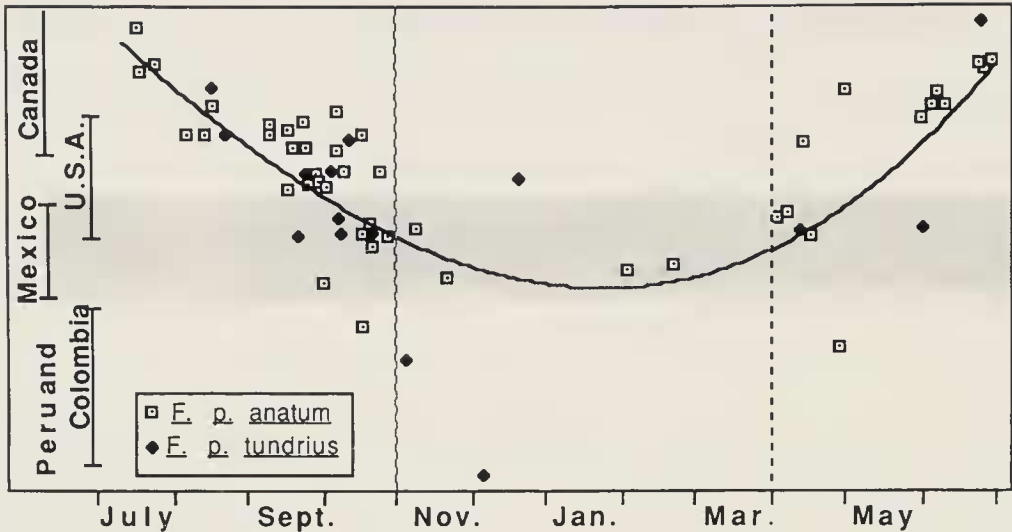


FIG. 3. Recoveries of *F. p. anatum* and *F. p. tundrius* according to date and latitude. Broken, vertical lines delimit winter months (see text) and stippling the maximum and minimum latitudes for Mexico.

between April 20 to May 3 (880 sightings; Dekker 1984). Six pairs of *F. p. tundrius* occupied territories in the Keewatin District of Canada's Northwest Territories by May 28, in each of three years (Court 1986).

For Prairie and Peregrine falcons, the species with a moderate sample of recoveries, migration appeared to progress more rapidly in spring than in autumn. The scatter of autumn recoveries suggests a lesser slope than the scatter of spring recoveries (Figs. 1 and 3).

Migration routes.—Ninety-six banded Prairie Falcons were recovered throughout the year from 0 to 1900 km from their natal or breeding sites (Fig. 4). Judging from the distribution of recoveries, Prairie Falcons used two migration routes and wintering areas. One route extended in a southeasterly direction, and another route southwesterly crossing the Rocky Mountains. To examine, in an *a posteriori* fashion, whether the Prairie Falcons moved southward in two distinct directions or in a broad band, we divided the recovery region in the United States into three parts. Of 28 Prairie Falcons recovered in the United States, none were recovered southeast of the Alberta banding area between longitudes 104 and 111°N (e.g., the eastern and western boundaries of Wyoming). This disparity was probably not caused by a bias in encounter and reporting rates, because eight of 17 other falcons reported from the western United States were found in this region ($\chi^2 = 16.03$, $P < 0.001$). Furthermore, Enderson (1964) saw wintering Prairie Falcons in this region.

Whether Prairie Falcons used an easterly or westerly route depended on their area of origin. Of 21 falcons that used the eastern grassland route, a greater proportion originated east of 111° longitude ($N = 14$) than west

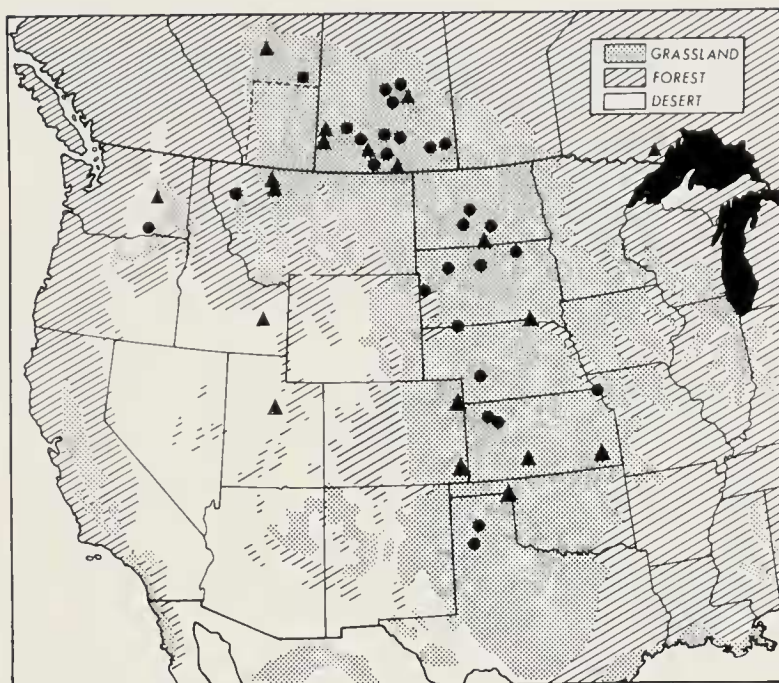


FIG. 4. Recovery locations of 48 Prairie Falcons are shown in relation to habitat and age. Circles represent individuals up to one year old, and triangles older individuals. Forty-eight additional individuals were recovered near their banding sites within the area bounded by a dashed line in southern Alberta. Of 96 falcons, nine were banded in Saskatchewan. Eighty-seven falcons were banded as nestlings and nine as adults.

of 111° longitude ($N = 7$). Of seven falcons that used the western route, six originated west of 111° longitude ($\chi^2 = 5.79$, $P = 0.016$).

Prairie Falcons that used the eastern migration route occupied habitat broadly categorized as grassland. Instead of flying directly southeast from Alberta, they apparently moved first due east into Saskatchewan and then south (Fig. 4). Once in the United States, 21 Prairie Falcons used a region (\bar{x} longitude = 101° , $SD = 3.3$) similar to 44 Ferruginous Hawks (*Buteo regalis*) (\bar{x} longitude = 103° , $SD = 3.4$) also banded in Alberta (Schmutz and Fyfe 1987). Both raptors used similar migration routes although their winter food habits are apparently very different. Horned Larks (*Eremophila alpestris*) are a primary winter food for Prairie Falcons (Enderson 1964, White and Roseneau 1970). Ferruginous Hawks probably rely on black-tailed prairie dogs (*Cynomys ludovicianus*; Schmutz and Fyfe 1987).

An affinity for grassland was also evident from the recovery locations of Prairie Falcons that moved southwesterly. Of seven individuals, five were recovered in or near grassland habitat even though this type of habitat is comparatively rare there. Only two Prairie Falcons were recovered in forest habitat; in western Ontario, and in the Black Hills of South Dakota.

Prairie Falcons banded in Alberta and Saskatchewan mixed extensively on migration and in winter with falcons banded in Wyoming. Although

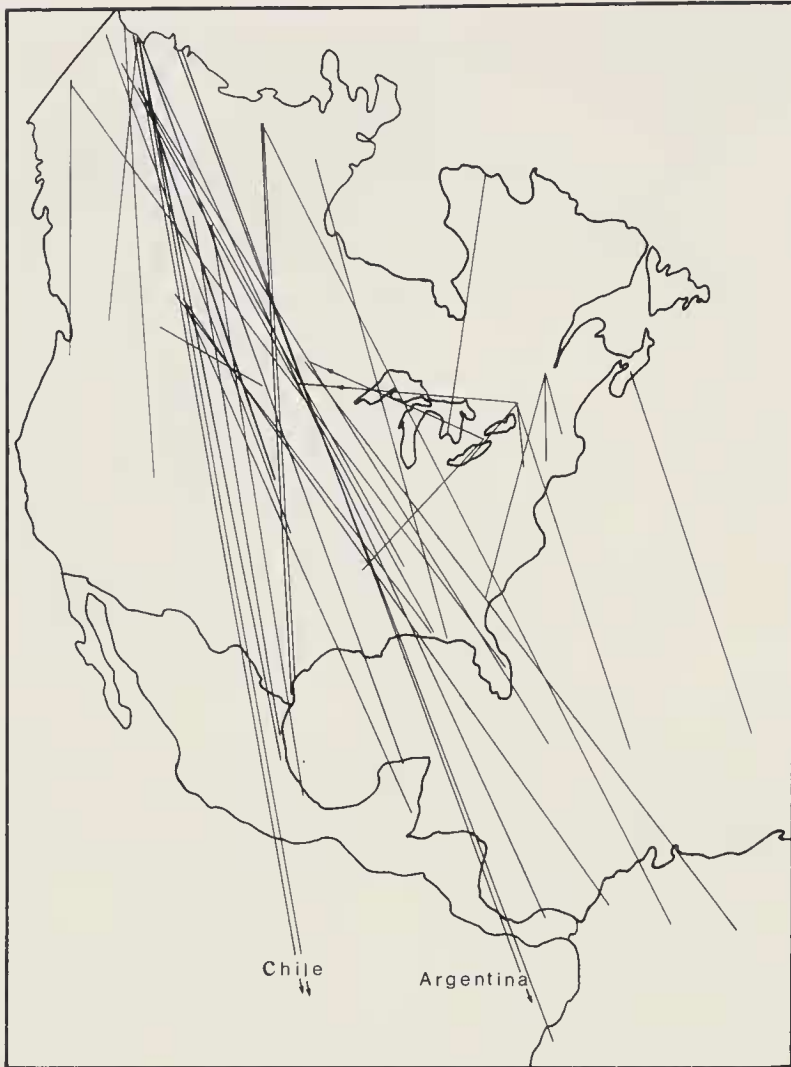


FIG. 5. Thirty-seven peregrine banding and their southerly recovery locations are connected via a straight line. Two northwesterly movements in North America are indicated by arrows. Three recovery locations near Iquique and Traiguén, Chile, and Neuquén, Argentina are not shown. Falcons live captured at the Texas ($N = 8$) and Maryland-Virginia coasts ($N = 7$) are also omitted.

27 Wyoming falcons (Enderson 1964) were banded at least 650 km south of where our 21 recovered falcons were banded, fall and winter recoveries did not differ along a north-south (Mann-Whitney $U = 258$, $P = 0.539$) nor an east-west axis ($U = 250.5$, $P = 0.605$). Seven of 27 Wyoming falcons recovered between October and February were actually found northeast of their breeding area, including two in Manitoba. Prairie Falcons banded in Idaho moved to higher elevations in late summer and also in a prevailing easterly direction. Seven of 13 recoveries/sightings were made east of the continental divide (Steenhof et al. 1984). Thus, few falcons from these subpopulations flew the shortest distance to their wintering areas. This suggests that vagrancy has advantages that outweigh

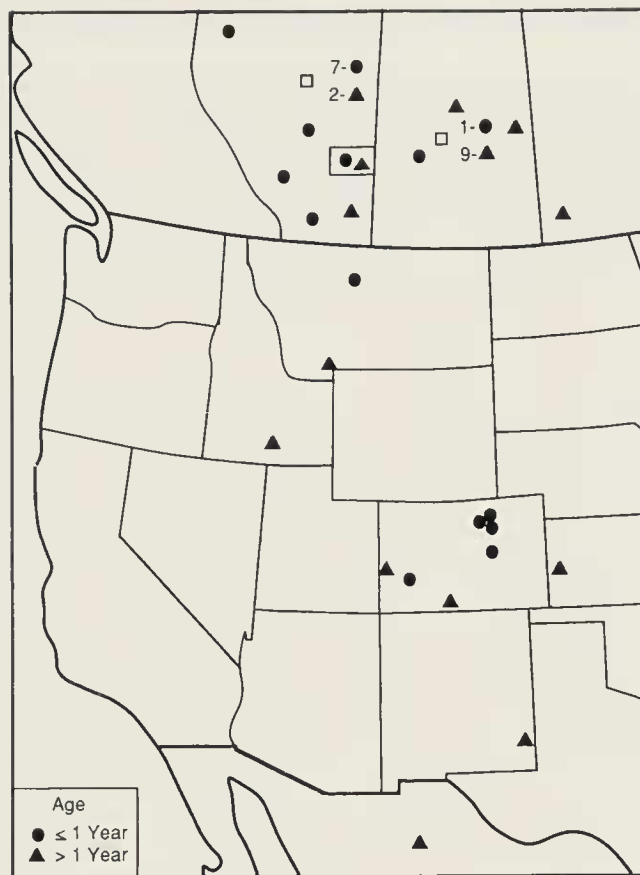


FIG. 6 Forty-three locations of Merlin recoveries are shown. Twenty-nine falcons were banded in southern Alberta, one near the Alberta boundary in southern Saskatchewan and 13 in the city of Saskatoon, Saskatchewan. One Merlin which was banded near the Arctic circle in the Yukon, was recovered in Costa Rica (not plotted).

the energetic cost associated with movement. Such vagrancy could result from falcons moving in random directions and stopping only when patchily distributed prey is encountered in abundance. Depending on the frequency of patches, some movements may be short, others long. Because of greater precipitation, grassland habitat may harbor prey in greater densities than desert-shrub habitat. This could explain the prevailing eastward movement.

A tundra Peregrine Falcon flew the longest distance. This falcon was banded at the mouth of the Mackenzie River in northern Canada and was recovered 12,000 km south near Traiguén in Chile. Most Peregrine Falcons were recovered southeast of their banding location (Fig. 5), although direction depended on where the falcons originated. Of 27 falcons from western Canada (W of 90° longitude) the movement was southeasterly with a mean of 137 degrees (SD = 17.4) from the banding/release site. The mean direction of eight falcons originating from eastern Canada was southwesterly with a mean of 226 degrees (SD = 47.4). One *F. p.*

pealei was recovered, in August, 200 km from its natal site in British Columbia.

Patterns of Peregrine migration were difficult to examine because of the different banding/release areas throughout Canada, the irregularly shaped continents, and two main methods of recovery, including live trapping at coastal beaches (e.g., Ward and Berry 1972, Henny et al. 1982) and reporting by the public. Nonetheless, several patterns are suggested by the data.

A Peregrine's affinity for coastal areas has been suggested by Enderson (1965), Bonney (1979), and by our data for the Central American coast (Fig. 5). Seven Peregrines were recaptured along the Atlantic coast in Maryland and Virginia. Recoveries suggest that northwestern Peregrines migrated over North American land masses but inhabited coastal regions in winter. During midwinter or the austral summer (November to February), 7 of 10 falcons were found within 60 km of coasts in Central and South America. Our band recovery data are of limited utility in assessing the degree of migration over sea, a route which some Peregrines are known to take (e.g., Kramer 1985). Not all coasts were used equally, however. Only one of our *F. p. anatum* was recovered near the Pacific Coast in North America. In South America no recoveries were reported from the South Atlantic Coast despite the occurrence of Peregrines there (Albuquerque 1984).

Thirty of 44 Merlins were found in Canada, 12 in the United States, 1 in northern Mexico and 1 in Costa Rica (Fig. 6). A cluster of recoveries in Colorado (6 of 11 U.S. recoveries) suggests that this region is an important winter area for the populations studied. Three individuals were recovered between Canada and Colorado, along the eastern edge of the Rocky Mountains in the United States. The banded Merlins were reared or breeding in the parkland habitat at the northern edge of the mixed-grass prairie, and were recovered in winter in the woodland habitat along the eastern foothills of the Rocky Mountains. Two Merlins banded in our banding region in 1930 and 1931 were recovered in Arizona (Lincoln 1936).

Of the kestrels banded in Alberta two were recovered again in Alberta and one in Michigan.

Falcon dispersion.—To examine the breadth of dispersion by falcons originating from Canada in relation to their respective species' winter range, we compared the distribution of recoveries with sightings made during Christmas bird counts (CBC) in 1981. We chose 1981 because at the close of this banding project the greatest number of banded falcons may have been alive. The recoveries used are those from the winter periods (Figs. 1–3).

TABLE 2

A COMPARISON BETWEEN THE NUMBER OF FALCONS COUNTED ON CHRISTMAS BIRD COUNTS AND THE NUMBER RECOVERED DURING WINTER (SEE FIGS. 1-3) IN THE WESTERN UNITED STATES. THE NUMBER OF FALCONS COUNTED IS REPORTED PER 1000 KM DRIVEN

	Km (×1000)	Prairie Falcon		Peregrine Falcon		Merlin	
		Counted	Recovered	Counted	Recovered	Counted	Recovered
Washington	10.7	0	2	0.6	0	4.1	0
Oregon	14.1	2.2	0	0.7	0	1.4	0
Idaho	4.3	7.9	2	0	0	0.7	1
California	46.7	3.1	0	0.6	0	1.2	0
Nevada	1.6	3.8	0	0.6	0	0	0
Utah	4.0	6.3	0	0	0	1.3	0
Arizona	8.0	6.1	0	0.1	0	1.4	0
Montana	7.0	2.4	2	0	0	0.9	2
North Dakota	6.1	0.8	1	0	0	0.5	0
South Dakota	5.1	0.8	3	0	0	1.0	0
Wyoming	4.5	1.8	0	0	0	0	0
Colorado	11.7	4.9	0	0	0	1.1	6
New Mexico	5.6	0	0	2.0	0	0.9	1
Nebraska	3.4	0	2	0	0	1.5	0
Kansas	4.3	6.7	4	0.5	0	1.2	1
Oklahoma	5.9	1.9	2	0.2	0	1.4	0
Texas	30.0	0.7	0	0.3	0	0.6	0
Total			18		0		11

Prairie Falcons were recovered in 8 of 17 states in the western United States (Table 2). The recoveries of Prairie Falcons by state did not differ significantly from the proportions suggested by CBC ($\chi^2 = 5.85$, $P = 0.054$, $df = 2$). In comparison to the small Canadian banding region, the vagrant falcons were spread over a recovery region that was many times larger. One Prairie Falcon exhibited remarkable winter site fidelity. This falcon was captured in Idaho in February at eight months of age and again 3 km away 12 months later.

Except for one *F. p. tundrius*, live-captured along the Virginia coast in December, none of our peregrines were recovered in the United States in winter. In comparison to Prairie Falcons, peregrines were rare on CBC in the western United States but were seen in nine of the 17 states shown (Table 2, see also Enderson 1965). These results suggest that most of the Canadian *F. p. anatum* and *F. p. tundrius* winter south of the contiguous United States.

Merlin recoveries were from five of the 17 states (Table 2). Merlins were seen on CBC in all but two of the western states, and the distribution of sightings differed significantly from the small sample of recoveries (χ^2

= 7.30, $P = 0.026$, $df = 2$). Six of our 11 recoveries were concentrated in Colorado, even though this state accounted for only 6% of all sightings (Table 2). Even if our banded Merlins, which originated from woodland habitat (aspen parkland), had restricted themselves to woodland habitat (Rocky Mountain foothills) on migration and in winter, their dispersion was narrower than may be expected based on available woodland habitat alone.

Migration versus residency.—Raptors as a group exhibit a diversity of dispersion patterns ranging from no migration to long distance movements (Newton 1979). Variability in the distance of migration, and partial migration by one sex or age group could be linked to food availability (e.g., Newton 1979).

Peregrine Falcons exhibited complete migration in this study in parallel with their waterfowl, shorebird, and songbird prey (Dekker 1984, Ward and Laybourne 1985). Gyrfalcons, Prairie Falcons, and Merlins exhibited partial migrations, consistent with the exodus of some avian prey from their arctic and subarctic environment, or the hibernation of mammalian prey (*Spermophilus* spp.). In winter, Gyrfalcons occupied previously used nesting areas and probably relied on Ptarmigan (*Lagopus* spp.) for food (Platt 1976, Poole and Bromley 1988). However, even falcons that remained in Canada moved some distance from their breeding or natal site. Four Gyrfalcons moved 900–2400 km prior to or during winter months. Gyrfalcon movements do not reach far south. This falcon was rarely recorded on CBC in the United States (<1% of 493 large falcons seen in 1981, Table 2) or in southern Canada (Houston 1985, Slater 1987, Wiseley and Pinel 1987). Six Prairie Falcons were recovered in Canada in winter 13–600 km ($\bar{x} = 288$ km) from their nests. We have no evidence that any Prairie Falcons actually remained in or near their original breeding or natal area. Casual visits to our study areas in winter indicate that the falcons had left their nesting area. Horned Larks, a primary winter food for Prairie Falcons (Enderson 1964, White and Roseneau 1970), winter only in extreme southern Canada (Salt and Salt 1976). Non-migratory Merlins are common in cities in prairie Canada and rare in rural areas (James et al. 1987). Merlin abundance in cities has increased since 1975, and this increase has been linked to a rise in the abundance of the Bohemian Waxwing (*Bombycilla garrulus*).

Age differences.—Raptor cohorts can exhibit “differential migration” (Terrill and Able 1988) according to differences in resource use (e.g., Kerlinger and Lein 1986). Since falcons obtain at least some of their prey through aerial pursuit, age-specific differences in wing shape and size (e.g., White 1968) may lead to different feeding strategies and hence different wintering areas. Ward and Laybourne (1985) found that adult peregrines

TABLE 3

RECOVERY OF FALCONS OF DIFFERENT SEX ACCORDING TO STAGE IN MIGRATION. TIME PERIODS CORRESPOND TO THOSE IN FIGS. 1 TO 3

	Late summer/ autumn	Winter	Spring/early summer	χ^2	<i>P</i>
Prairie Falcon					
Females	7	19	6	9.69	0.008
Males	14	5	4		
Peregrine Falcon					
Females	17	4	6	0.75 ^a	0.784
Males	10	3	4		
Merlin					
Females	2	7	—		
Males	1	2	—		

^a *df* = 1.

consumed a significantly greater proportion of shorebird prey on migration than did immature peregrines.

The distributions of recoveries of adult and immature Prairie Falcons and Merlins (Fig. 4) were similar at the regional level. For Prairie Falcons the sample of winter recoveries (November to February, *N* = 24) was sufficiently large to permit a statistical comparison. We found no significant deviation from random north-south dispersion between age classes (Wald-Wolfowitz *T* = 13, *P* = 0.225; Conover 1971). This is consistent with the field observations of White and Roseneau (1970) who found that immature falcons comprised 64% of 70 encounters (but see Enderson 1964). Our data were insufficient, however, to determine whether clusters of locally separate age groups existed within the broad winter range used by this species or whether differences in the proportions of adults to immatures existed between years.

During the summer period we received no recoveries from the southern portions of the species' ranges. This suggests that even though some individuals may not attempt to breed during their first summer, they undertook a return migration.

Sexual differences.—Variation in migration pattern between the sexes may arise from differences in the timing of a return migration (e.g., Ketterson and Nolan 1976) or from differences in resource use according to body size. Significantly more male Prairie Falcons were recovered in late summer and autumn than in winter and spring (Table 3). The sex ratio had changed sufficiently so that only five males were recovered in winter

compared to 19 females. White and Roseneau (1970) captured 32 females and only four males in north central Utah in winter, corroborating that the sex ratio is imbalanced. Although all five males were recovered in the northern half of the winter latitudes compared to 11 of 19 females, this difference was not statistically significant ($\chi^2 = 3.16$, $P = 0.076$). These results suggest that the north-south gradient in recoveries of male Prairie Falcons was due to a greater mortality among males in late summer, and not to a difference in dispersion according to sex.

There was no difference between the sexes in the recovery of peregrines by season (Table 3), nor in their dispersion. The proportion of males and females above the line depicting the average progress of migration over time (Fig. 3; 9 males, 14 females) was nearly identical to the proportion located below (8 males, 13 females).

"Leap-frog" migration.—In some populations of migratory raptors, members of a northerly breeding segment winter farther south than a southern segment (Wallin et al. 1987). Two merlins banded in this study were recovered south of the United States, one in northern Mexico and one in Costa Rica. This Costa Rican recovery was the only recovery of merlins banded in the boreal forest of northwestern Canada and suggests that these northern Merlins (*F. c. bendirei*; Godfrey 1966) fly over the breeding and wintering grounds of *F. c. richardsonii* and winter in Central and South America. Clark (1985) received recoveries of 18 Merlins from Florida and the Greater Antilles. Although these falcons were banded on migration at Cape May Point, New Jersey and their breeding area was not known, this corroborates that Central America is an important wintering ground for Merlins.

To examine potential differences on migration between subpopulations, we examined recoveries of members of different subspecies. *F. p. tundrius* migrated further south than did members of *F. p. anatum*. The average recovery latitude of 15 falcons found in Central or South America, or reported freshly killed during November through February in North America, was 17°N (SD = 17.4, N = 8) for *F. p. anatum* and 2°S (SD = 27.7, n = 7) for *F. p. tundrius*. Despite the near disappearance of the southern breeding *F. p. anatum*, the northern breeding *F. p. tundrius* have not significantly invaded the wintering range of *F. p. anatum* as would be expected if competition were a major factor in determining the winter location of the two subpopulations.

Peregrines breeding in Canada are outside of Canada for seven months of the year. Their annual distribution includes many countries which makes conservation management an international challenge. In the late 1970s and early 1980s, after the use of DDT was banned in North America, spring migrants returned from Latin America with significantly higher

concentrations of DDE than the concentrations with which fall migrants departed (Henny et al. 1982). This international residency may pose a greater threat to Canadian falcons which appear to migrate farther south (Fig. 3) than do falcons released in the continental United States. Only one of nine recoveries of falcons banded in the United States (Barclay and Cade 1983) was reported south of the continental United States.

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